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Hydrological seasonality and benthic algal biomass in a Neotropical floodplain river

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Abstract. Our study evaluated spatiotemporal variation of physicochemical parameters and benthic and sestonic algal biomass in littoral areas of the main channel and floodplain lakes of the Cinaruco River, a lowland tributary of the Orinoco River in Venezuela. The Cinaruco is characterized by a highly predictable annual flood pulse, high transparency, and extremely low conductivity and suspended sediment load. During 2002 and 2003, 10 sites in the main channel and floodplain lagoons were sampled on 12 occasions. Correspondence analysis based on water physicochemical variables and algal biomass showed that ~80% of the variation in the multivariate space among sites and sampling dates was explained by 2 axes. During the high-water periods, river and lagoon sites showed high similarity in water variables and algal biomass. Conductivity, SiO_3, and chlorophyll *a* concentrations (both benthic and sestonic) were low during the high-water phase. On the other hand, water variables and algal biomass differed between river and lagoon sites during the low-water period. The absence of flow in lagoons and consistently low algal biomass (sestonic and benthic) in river sites were the most important features of the spatial variability between main channel and lagoon sites during low-water phases. Benthic chlorophyll *a* was highly uniform at small spatial scales and significantly heterogeneous at large spatial scales. The annual flood regime of the Cinaruco, which drives the concentrations of dissolved materials and affects material interchanges between aquatic and terrestrial systems, also appears to be responsible for creating strong patterns of seasonal and spatial variation in benthic algal crops.

Key words: flood pulse, seasonality, hydrological connectivity, nutrients, chlorophyll *a*, Cinaruco River, Orinoco Basin, Venezuela.

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The study of aquatic–terrestrial transition zones in floodplain systems has received greater attention in recent years than in the past, especially given the role of these areas in maintaining biodiversity and mediating interchanges of materials and energy between

aquatic and terrestrial habitats (Ward and Standford 1995, McClain and Elsenbeer 2001). The pervasive influence of periodic flood pulses on ecosystem processes within tropical floodplain rivers has been widely recognized (Junk et al. 1989, Lewis et al. 2000). Water-column processes have been examined in several Neotropical rivers, including the Amazon and Orinoco (Lewis et al. 1995). However, ecological dynamics of benthic components in response to seasonal flood pulses remain poorly documented (Lewis et al. 1995). The ecology of the zoobenthos has been studied in several large Neotropical floodplain rivers (e.g., Walker et al. 1991, Junk and Robertson 1997, Ezcurra de Drago et al. 2004), but very little research has examined benthic algae in these systems.

As far as we know, no works have been published on epipelic algae (those living in and on sediments) of large lowland rivers in the Neotropics. Most research thus far has focused on algae that colonize artificial substrates or attach to leaves and roots of submerged or floating vegetation (Engle and Melack 1993, Putz and Junk 1997). Given the much larger surface area of sediments compared to woody debris or other substrates and the potential contribution of algal biomass to food webs in river–floodplain ecosystems (Lewis et al. 2001, Thorp and Delong 2002), studies that focus on epipelic algal dynamics are needed to understand better the role of autochthonous C inputs to these systems.

Spatial heterogeneity in natural systems plays a critical role in the maintenance of species diversity and ecosystem processes (Pringle et al. 1988, Levin 1992, Cardinale et al. 2002). Organisms can influence spatial variation in ecosystems via physical disturbance or consumption. For example, spatial heterogeneity of benthic habitats in tropical streams is strongly influenced by grazing fishes that function as ecosystem engineers, and heterogeneity of periphyton communities (over scales of cm–m) is maximized at intermediate grazer densities (Flecker and Taylor 2004). Such findings have broad implications for how we interpret data collected over variable spatial scales. For example, is heterogeneity of benthic algae influenced by changes in the physical environment or activities of grazing fish? How might spatial heterogeneity affect the functioning of benthic algae as an autochthonous C source supporting the food web? These questions are especially pertinent in lowland rivers with extensive floodplains that support large populations of migratory grazing fishes (Winemiller and Jepsen 1998, Winemiller et al. 2006).

Here, we describe the temporal variations of physicochemical parameters and algal biomass of littoral areas of floodplain lakes and the main channel of the Cinaruco River. We also examine the spatial variability of benthic algal biomass using a nested sampling design that incorporates multiple spatial scales. Seasonal and spatial patterns in physicochemical variables and algal biomass were expected to occur as a result of the annual flood pulse of the Cinaruco, which modulates water retention times and the interchange of materials between terrestrial and aquatic habitats. We expected greater spatial heterogeneity in substrates and benthic algal biomass during high-water periods, when there was increased mobility of the aquatic–terrestrial transition zone, than during low-water periods. Our study contributes to our understanding of the ecology of highly dynamic and poorly known aquatic–terrestrial transition zones of tropical floodplain rivers.

Study Site

The Cinaruco River is a 505-km-long lowland tributary on the left-bank of the Orinoco River with an estimated basin area of 11,700 km^2 shared between Colombia (11%) and Venezuela (89%) (Fig. 1). The Cinaruco meanders entirely on the vast tectonic subsidence system of the Orinoco llanos.

The climate in the region is a typical tropical wet/dry climate dominated by the northeast trade winds and the north–south migration of the Intertropical Convection Zone (ITCZ). Annual mean temperatures average ~25 to 26°C with annual rainfall averaging ~1300 mm (Sarmiento and Pinillos 2001). The wet season is from May to November (peaking in June–July). This seasonality in precipitation determines the flood dynamics of rivers draining the western llanos.

According to Sarmiento's (1983) classification of neotropical savannas, the landscape in the vicinity of our study site consists of hyperseasonal and seasonal grassland savannas. Vegetation of the seasonally flooded terrain is mostly composed of C_4 grasses and sedges with isolated small trees, and a dense gallery forest belt is evident along watercourses. Maintenance and productivity of savanna vegetation are regulated by complex interactions among soil characteristics, fire, and water availability (Medina and Silva 1990).

The Cinaruco is one of the few large left-bank tributaries of the Orinoco not having its headwaters in the Andes Mountains. Rivers such as Cinaruco that originate entirely or mostly within the llanos have low nutrient and suspended sediment loads because of the dystrophic character of llanos soils (Medina and Silva 1990).

Our study area was located in an ~12-km stretch of river in a floodplain area with high geomorphological heterogeneity (Fig. 1). This area is 40 km from the

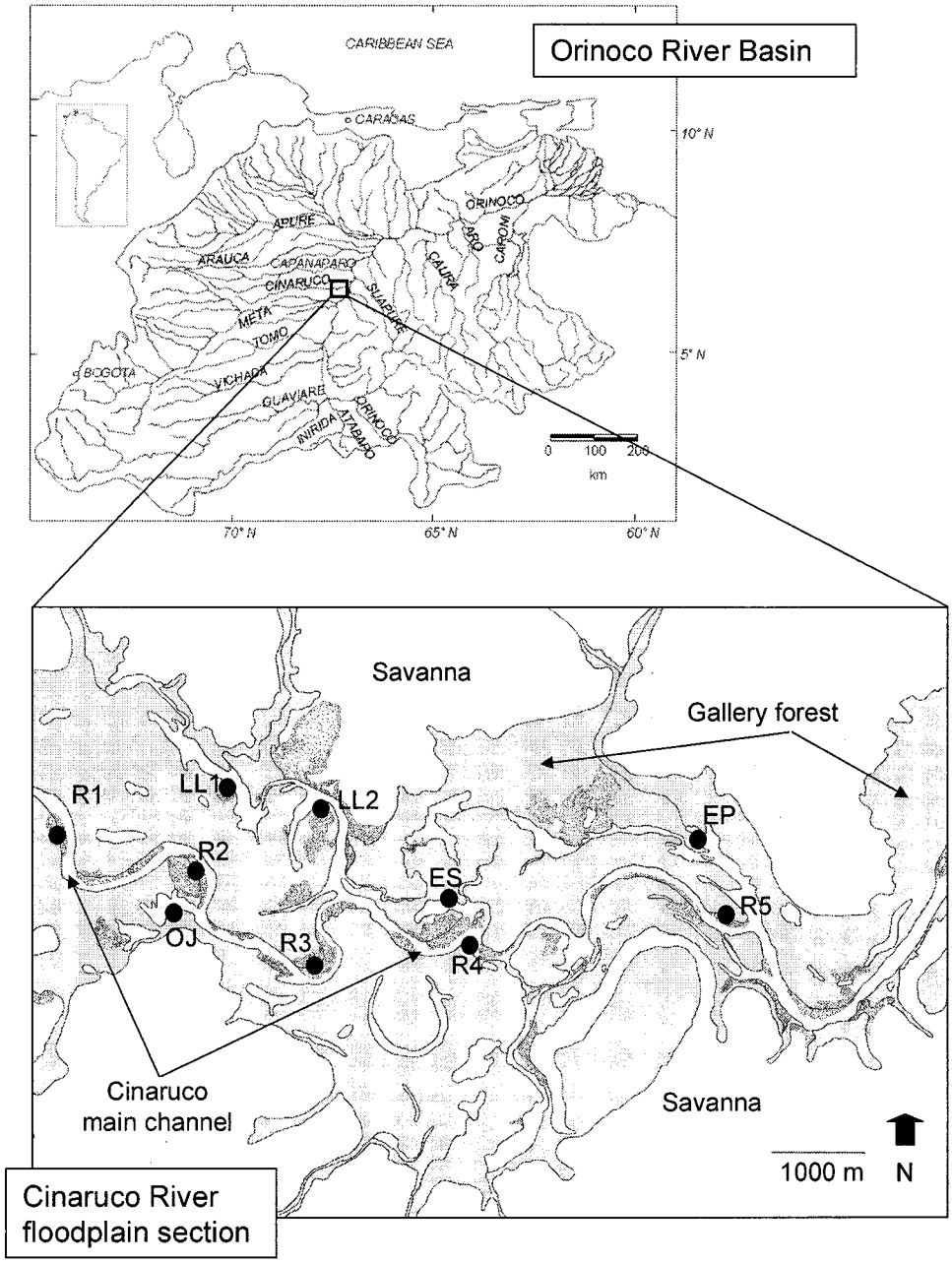

FIG. 1. Study area showing the location of Cinaruco River in the Orinoco River Basin and the location of sites (R = river, LL = Laguna Larga, EP = Laguna Espiñero, ES = Laguna Esse, OJ = Laguna Ojero) for the monthly sampling design. Savanna and the gallery forest are also shown.

confluence of the Cinaruco with the Orinoco and shows a high degree of meandering. The width of the gallery-forest belt ranges from a few meters to >2 km, with the widest forests located in areas containing many floodplain lakes. A variety of floodplain lakes of diverse origin (oxbows, permanently connected lakes, abandoned channels, and natural depressions) are found in the area.

Methods

Site selection and sampling strategy

Our river sites (R1–R5) were located on exposed point sandbars along the main channel of the river (Fig. 1). Our lagoon sites were located in 4 floodplain lakes that were continuously connected with the main channel. Two sites were located in Laguna Larga (LL1

and LL2), and one each in lagunas Espiñero (EP), Esse (ES), and Ojero (OJ) (Fig. 1). Sites were chosen along sandy shores with a smooth slope and lacking submerged large woody debris or rocks.

Logistical restrictions associated with seasonal variation in water level constrained the placement of sampling sites within the littoral zone of the main channel and floodplain lakes. The land–water margin moved several kilometers along the riparian elevational gradient during the wet season. Monthly sampling occurred from January to May 2002 and from December 2002 to July 2003 (12 sampling dates) for physicochemical variables and sestonic chlorophyll *a* (S-CHLA) and phaeophytin *a* (S-PHAE). Seven of our sampling dates corresponded to the low-water period (Jan–Apr 2002, Feb–Apr 2003), and 5 sampling dates corresponded to the high-water period (May and Dec 2002, May–Jul 2003). Benthic samples for chlorophyll *a* (B-CHLA) and phaeophytin *a* (B-PHAE) determinations were taken on every sampling date except for July 2003, when the shoreline at many sampling sites had moved a considerable distance landwards and benthic sampling was not possible in riparian forests.

Hydrological assessment

A hydrograph of the Cinaruco River was constructed from daily stage-height readings at Laguna Larga (Fig. 2) and 2 natural periods were identified. The low-water period was characterized by low water levels, exposure of point sandbars, and almost no water flow in floodplain lakes, whereas the high-water period was defined by water flow in the floodplain lakes and submergence of point sandbars in the main channel. During the peak of the high-water period (late July), the connection of the river with its floodplain attained its maximum, with extensive areas of savanna inundated. The water-level threshold that discriminated the 2 hydrological periods was 290 to 320 cm (Fig. 2).

Analytical methods

Water samples and in situ water-column measurements were taken at a depth of 30 cm below the water surface in the littoral zone (1-m depth). For every site and sampling date, in situ measurements were made of flow (mechanical flow meter), temperature and dissolved O_2 (YSI 95 O_2 meter), transparency (Secchi disk), conductivity, and pH (Hydrolab MiniSonde). Water samples were filtered through GF/F Whatman glass fiber filters and NH_4, NO_3, NO_2, urea, soluble reactive P (SRP), and SiO_3 concentrations were measured using autoanalyzer technology (Grasshoff et al. 1983). Detection limits achieved with a Technicon II Autoanalyzer were 0.089 μM NO_3, 0.009 μM NO_2,

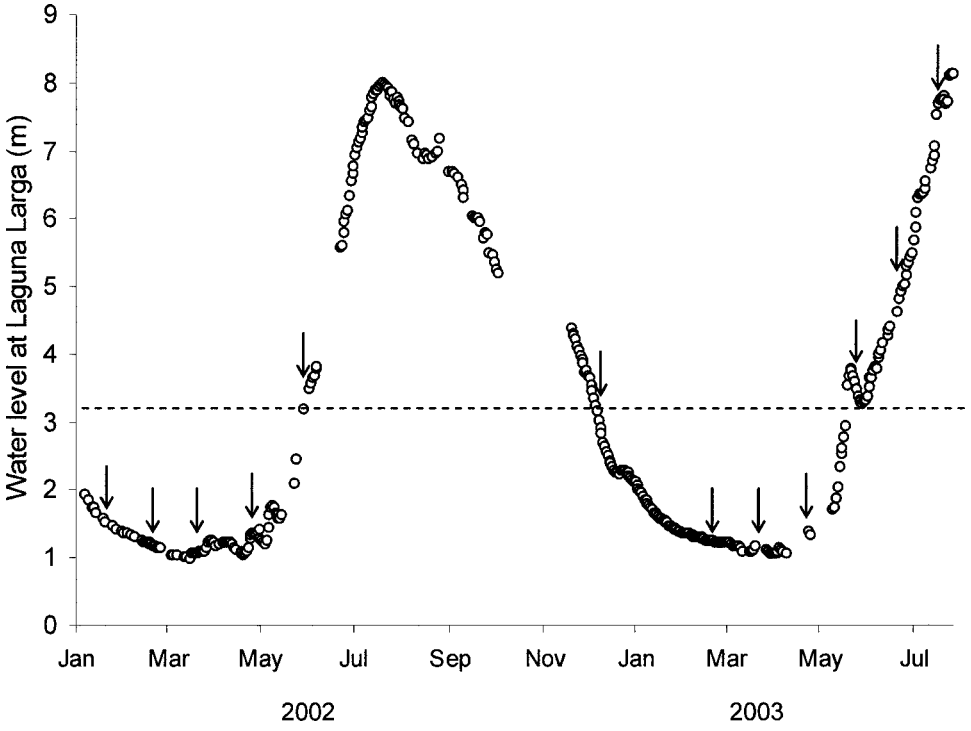

FIG. 2. Hydrograph of Cinaruco River at Laguna Larga during 2002 and 2003. The dashed line shows the approximate depth used to discriminate between the periods of low- and high-water in the floodplain. Arrows mark sampling dates.

0.035 μM NH_4, 0.161 μM urea, 0.024 μM PO_4, and 0.071 μM SiO_3. Triplicate water samples for determinations of S-CHLA and S-PHAE were filtered in situ through Whatman GF/F glass fiber filters. Triplicate sediment core samples to examine B-CHLA and B-PHAE were taken using a small plastic Petri dish (5-cm diameter and 1.3-cm height) at a depth between 0.7 and 1 m. A Petri dish was pushed into the substrate, and a spatula was placed under the Petri dish to trap the contents during retrieval. The filters and Petri dishes were kept frozen and stored in the dark until analyses were performed. S-CHLA, S-PHAE, B-CHLA, and B-PHAE were determined using the overnight 90% acetone extraction protocol using spectrofluorometric and spectrophotometric methods (APHA 1998). All chlorophyll *a* values were corrected for phaeophytin *a*.

We used a hierarchical sampling design to analyze the spatial variation of B-CHLA at different scales within a section of the floodplain of the lower Cinaruco River. Our sampling scheme incorporated 4 spatial scales, ranging from the kilometer scale to the decimeter scale. Selection of survey sites in floodplain habitats (km scale) was not random because of logistic constraints. Thus, macrohabitat was regarded as a fixed variable in our model, and subordinate random factors were nested within it. Subordinate factors included 3 shores within each habitat at the 100-m scale, four 2 × 2 m plots within each shore at the 1- to 10-m scale, and 3 samples (small Petri dishes) within each plot at the 0.1-m scale. This sampling design was carried out during periods of low water (March 2002) and high water (May 2002).

Data analyses

Bivariate correlations were run between biotic variables (S-CHLA, S-PHAE, B-CHLA, and B-PHAE) and abiotic parameters for river and lagoon monthly survey data subsets. Pearson product–moment correlation analysis was done using SPSS (version 11.5, SPSS, Chicago, Illinois).

Sampling dates and sites were ordinated based on the measured environmental variables plus sestonic and benthic CHLA and PHAE using correspondence analysis (CA), an indirect gradient technique, in CANOCO (version 4.0, Microcomputer Power, Ithaca, New York).

A 3-factor nested analysis of variance (ANOVA) was used to analyze the spatial variation of B-CHLA at different scales. Data were transformed using the $(x+1)^{0.5}$ transformation to satisfy the homocedasticity of variances assumption. Variance components were calculated for all random factors as described in Underwood (1997). Nested mixed ANOVA was done following Sokal and Rohlf (1995), and normality plots were run using SPSS version 11.5.

Results

Hydrological and physicochemical variables

The hydrological regime of the Cinaruco showed a typical monomodal pattern exhibited by large rivers with a dry–wet climate (Fig. 2). The water level at Laguna Larga had a 7-m difference between minimum and maximum depths recorded over the 2 y of sampling. During both years, minimum levels occurred during the first 2 wk of March, and highest levels occurred during the last 2 wk of July. From mid January to April of each year, the water level changed little, with values close to the minimum. During May, at the beginning of the rainy season in the area, the water level increased markedly (~2 m in 20–25 d). Striking fluctuations (negative or positive) of >0.3 m in <24 h occurred several times during this period. Water-flow patterns along the margins of the river and inside the lagoons changed as water level rose. Floodwater did not reach the upland savanna until June and remained there until late September. By late October to mid November, the waters had receded enough to expose the sandy beaches in the river's main channel. During this transitional period of descending waters, sudden changes in water level (like those observed during the rising-water phase) were also common. The rate of water-level change was lower for the descending limb of the hydrograph than for the rising limb.

Fluctuations in physicochemical variables in the littoral areas of floodplain lakes and river sites largely reflected the seasonal hydrological regime of the Cinaruco (Figs 3, 4). Water temperature varied inversely with water level, with highest temperatures (~33°C) during the late low-water season and minimum values (~27–28°C) during inundation (Fig. 3A). Temperature was generally lower at river sites than in lagoons. Dissolved O_2 ranged from 4.3 to 8.5 mg/L with the highest values during the low-water period and minimum concentrations during the high-water period (Fig. 3B). Water flow varied seasonally in both river channel and lagoon sites (Fig. 3C). Water flow in littoral channel sites averaged 27.3 ± 1.77 cm/s (mean ±1 SE) during low-water phases and 22.4 ± 3.63 cm/s during high-water. Highest values (>40 cm/s) were recorded at the beginning and at the end of the period of high-water (May and December 2002, respectively). A large reduction in flow at river sites was observed starting in June 2003 when flow averaged 6.2 cm/s and again in July 2003 when there was no flow. This reduction does not indicate that

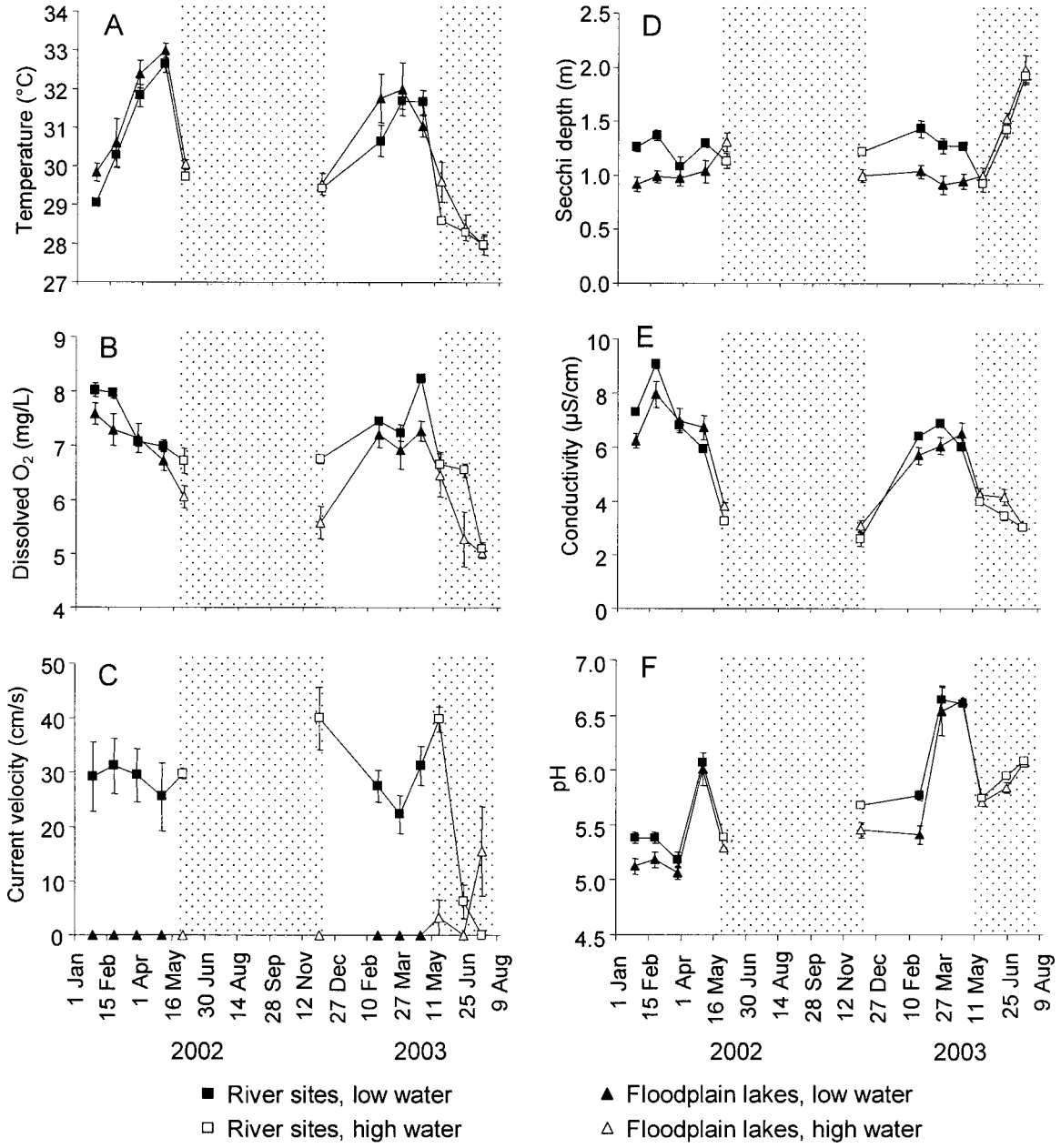

FIG. 3. Mean (±1 SE) temperature (A), dissolved O_2 (B), water flow (C), Secchi depth (D), conductivity (E), and pH (F) calculated across 20 mo for river sites ($n = 5$) and floodplain lakes ($n = 5$). Shaded areas indicate high-water periods.

water flow stopped in the entire river, but only at our littoral survey sites. We did not detect flow in the lagoons on any of the low-water sampling dates. Throughout the low-water period, Secchi depth averaged between 0.8 to 1.1 m for lagoons, and between 1.1 and 1.4 m for river sites (Fig. 3D). Higher values usually were found during the high-water period. Conductivity and pH also changed with the water level (Fig. 3E, F). At the onset of the high-water period in May, both conductivity and pH declined sharply. Conductivity remained low during the remainder of the high-water season, whereas pH steadily increased after the first month of inundation. Conductivity values were remarkably low in both lagoon and river sites. Maximum values were never >9.4 and 5.2 µS/cm during low and high-water periods, respectively. Recorded pH in the river and lagoons ranged between 5 and 7.

Dissolved nutrients and SiO_3 showed large fluctuations, but patterns were not strongly seasonal (Fig. 4A–D). In general, nutrient concentrations in lagoons were similar to values recorded at river sites.

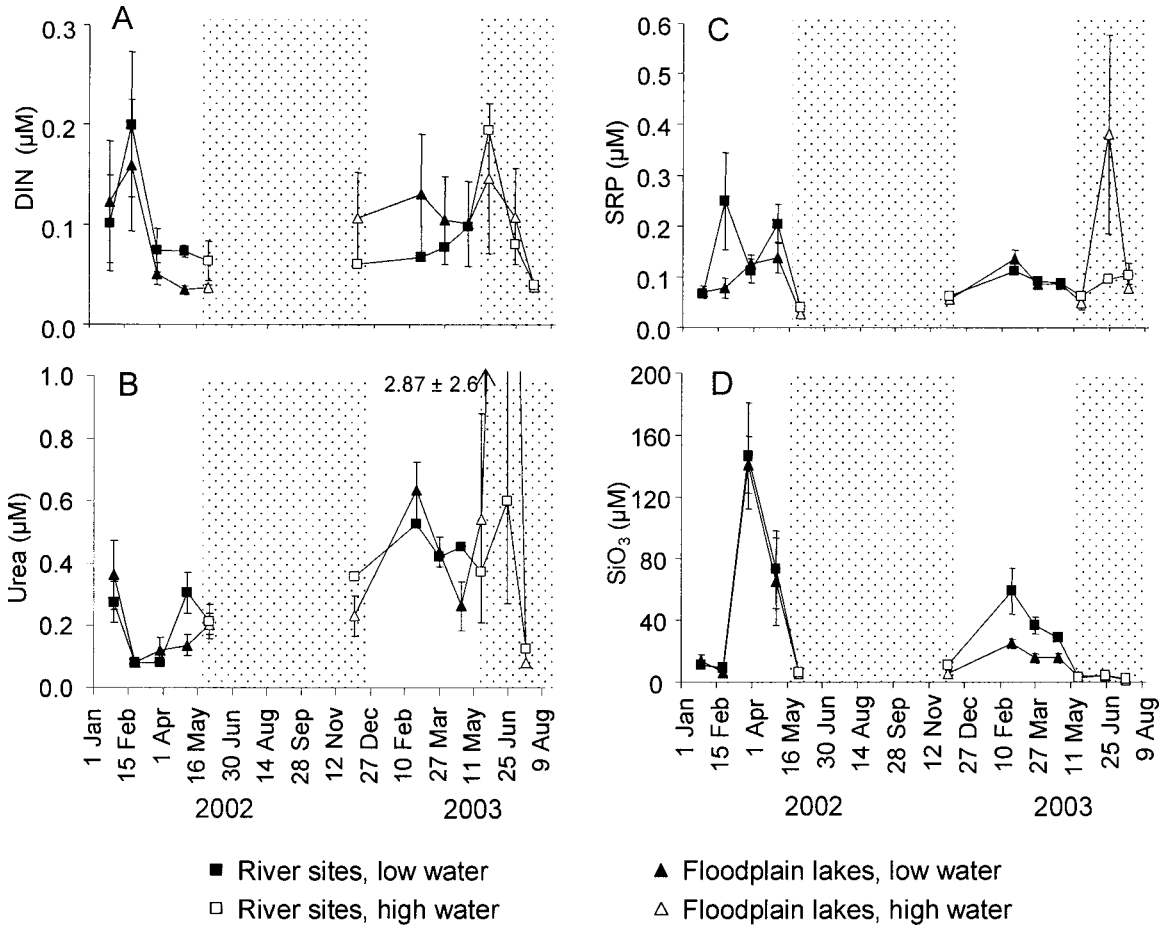

FIG. 4. Mean (±1 SE) dissolved inorganic N (DIN) (A), urea (B), soluble reactive P (SRP) (C), and dissolved SiO_3 calculated across 20 mo for river sites ($n = 5$) and floodplain lakes ($n = 5$). Shaded areas indicate high-water periods.

Monthly average values for dissolved inorganic N (DIN = $NO_3 + NO_2 + NH_4$) and urea ranged from 0.1 to 0.6 μM (Fig. 4A, B). Particularly notable was the consistent low concentration of NO_3 at all sites (data not shown). February 2002 was the only period in which NO_3 values were above the detection limit (>0.089 μM). NH_4 usually accounted for >50% of DIN. Around 30% of the measured values for NH_4 and urea fell below their detection limits (data not shown). An increase in DIN concentrations at the beginning of the flood period was observed during the 2nd y, but not during the 1st y. Another DIN peak was observed in February 2002 (middle of the dry season).

SRP concentrations were similar between river and lagoon sites as well as hydrological periods (Fig. 4C). Dissolved SiO_3 was more dynamic, with peaks during low-water periods, and very low concentrations during inundation periods (Fig. 4D). The SiO_3 peak in both lagoon and river sites during late March 2002 coincided with the first local rainstorm. SiO_3 values increased by 2 orders of magnitude, from values as low as 3 μM in February 2002 (average values of 6.03 and 8.72 μM for lagoons and river, respectively) to concentrations >210 μM at one of the river sites (average values of 141.02 and 146.78 μM for lagoons and river, respectively). None of the recorded values for SiO_3 fell below the method detection limit, and only <5% of the values for NO_2 and PO_4 were below detection limits.

Sestonic and benthic CHLA and PHAE

S-CHLA and S-PHAE concentrations in lagoons were always higher than those in river sites (sometimes 3× differences; Fig. 5A, B), except for the period of high water when concentrations in the river and lagoons were similar. S-CHLA was inversely correlated with the water level in both river and lagoon sites ($r_{river} = -0.781$, $r_{lagoons} = -0.868$, $p < 0.001$). S-CHLA was positively correlated with temperature, dissolved O_2, conductivity, and dissolved SiO_3 in river and lagoon sites (range of r values between 0.55 and 0.73 with all $p < 0.001$).

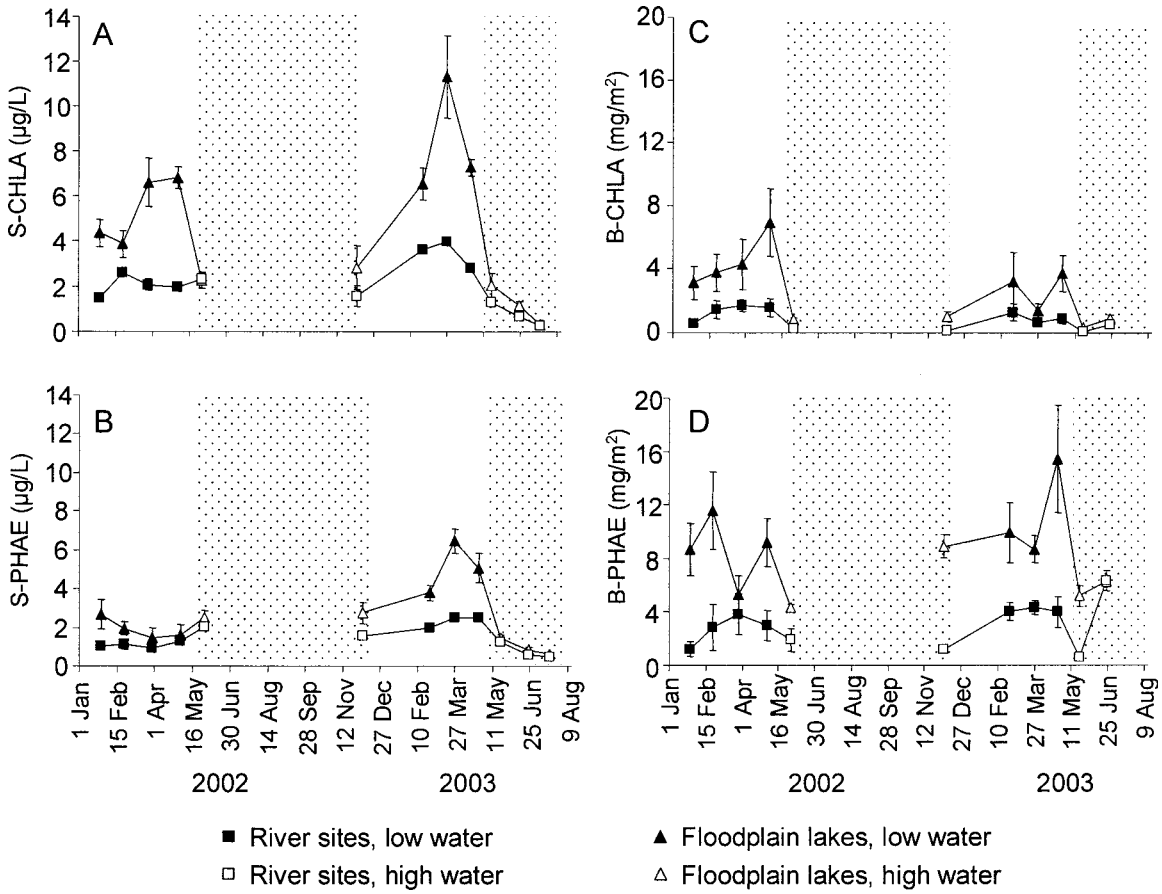

FIG. 5. Mean (±1 SE) of seston chlorophyll *a* (S-CHLA) (A), seston phaeophytin *a* (S-PHAE) (B), benthos chlorophyll *a* (B-CHLA) (C), and benthos phaeophytin *a* (B-PHAE) (D) calculated across 20 mo for river sites ($n = 5$) and floodplain lakes ($n = 5$). Shaded areas indicate high-water periods.

B-CHLA also was higher in lagoons than in river sites (Fig. 5C). Like S-CHLA, B-CHLA declined rapidly at the beginning of the high-water period. B-PHAE was always higher than B-CHLA (Fig. 5D). B-CHLA in river and lagoons showed the same significant relationships with abiotic variables observed for S-CHLA. However, B-CHLA was negatively correlated with flow in the river sites ($r = -0.470$, $p < 0.001$), but not in lagoons. S-PHAE and B-PHAE correlations with abiotic variables were similar to those of S-CHLA and B-CHLA, respectively, except that relationships were weaker.

Ordination

CA based on physicochemical variables plus sestonic and benthic CHLA and PHAE revealed 2 strong environmental gradients (Fig. 6). Eigenvalues for the first 2 CA axes were 0.246 and 0.073 (total inertia = 0.402), indicating the 1st and 2nd axes of the CA accounted for 61.3% and 18.2% of total variation among sampling dates and sites, respectively. Axis 1 was positively correlated with concentrations of SiO_3 and B-CHLA and negatively correlated with water level. The 2nd axis was positively correlated with water flow, and negatively correlated with B-CHLA, B-PHAE, and S-CHLA.

Hydrological periods were well separated along the 1st axis, and habitats (lagoon vs river) were separated along the 2nd axis (Fig. 6). Thus, we were able to distinguish 4 groups based on attributes of physicochemistry and chlorophyll concentrations: lagoons at low water, lagoons at high water, river sites at low water, and river sites at high waters. Among chemical variables, dissolved SiO_3 was particularly important in separating sites into high-water and low-water groups along the 1st axis. Samples with highest positive axis-1 scores corresponded to late March 2002 (following the first storm of the year). B-CHLA had a large influence on both multivariate gradients that separated sites and sampling dates according to hydrological seasons and habitats.

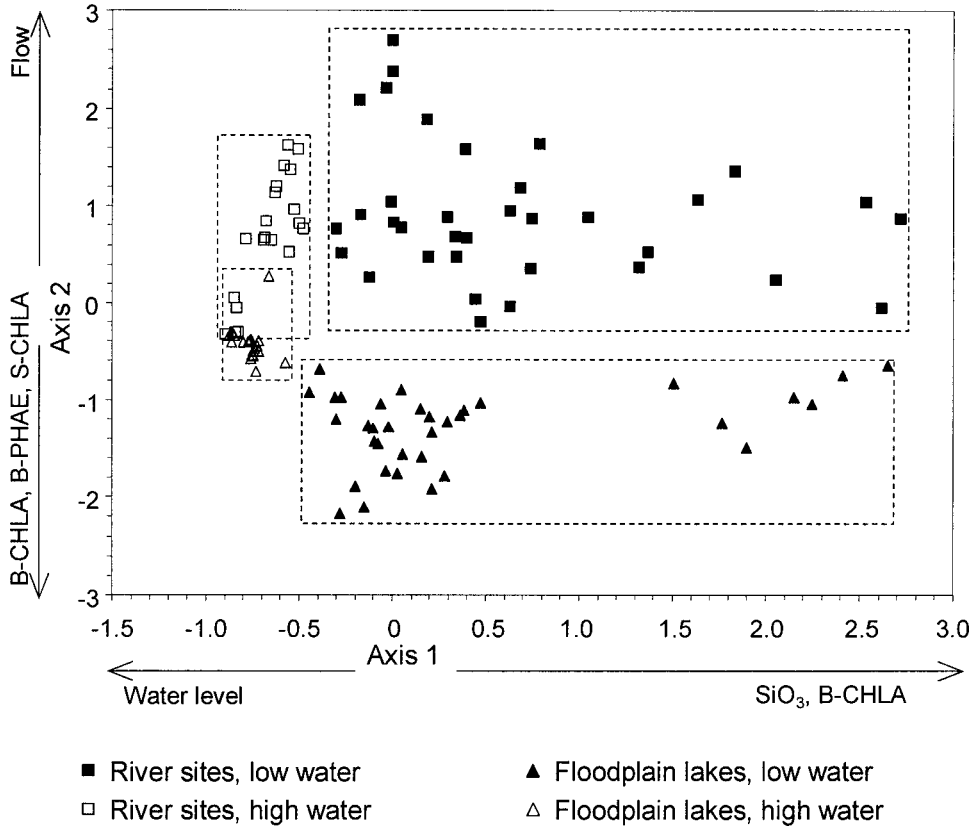

FIG. 6. Correspondence analysis ordination plot of the sampling sites and dates, based on physicochemical variables, seston chlorophyll *a* (S-CHLA), seston phaeophytin *a* (S-PHAE), benthos chlorophyll *a* (B-CHLA), and benthos phaeophytin *a* (B-PHAE). Subgroups based on habitat (floodplain lakes or river) and sampling periods (during low or high water) are enclosed with dashed lines. The first 2 axes explained 79.5% of the variation among sampling dates and sites. The most important variables contributing to each axis appear next to the arrows.

Spatial variability of B-CHLA

Significant variation in B-CHLA was found at the within-habitat, between-site level (shores) in hierarchical samples collected during both March and May 2002 ($p < 0.001$; Table 1, Fig. 7A, B). Within-habitat variation accounted for >95% of total variance. There was no significant effect of between-plot variation on B-CHLA during March. However, May samples revealed significant variation of B-CHLA between plots within habitats ($p < 0.001$; Table 1, Fig. 7B), although the proportion of total variance explained by between-plot variation was only 0.7%. The size of the residual variance was unexpectedly small for both months (3.6% and 0.6% for March and May, respectively), suggesting that patchiness at our smallest scale (Petri dishes) was negligible. March results imply that during the period of low water, processes controlling the distribution of algal biomass on substrates were spatially uniform at intermediate and small scales (at plot and Petri dish level), but were not uniform across larger scales (among shores).

Discussion

Variability in physicochemical variables

Hydrologic seasonality was strongly associated with variation in all of the physicochemical variables we

TABLE 1. Summary of nested mixed analysis of variance for benthic chlorophyll *a* (B-CHLA). Data were transformed before analysis as $(x+1)^{0.5}$. *** = $p < 0.001$, % variance = variance components estimates.

Source	df	MS	*F*	% variance
B-CHLA (March 2002)				
Habitat	1	20.59	10.57	–
Shore (habitat)	4	1.947	12.53***	95.5
Plots (shore[habitat])	18	0.155	1.70	0.9
Samples/residual	48	0.091		3.6
B-CHLA (May 2002)				
Habitat	1	9.11	1.56	–
Shore (habitat)	4	5.853	27.49***	98.7
Plots (shore[habitat])	18	0.213	4.89***	0.7
Samples/residual	48	0.043		0.6

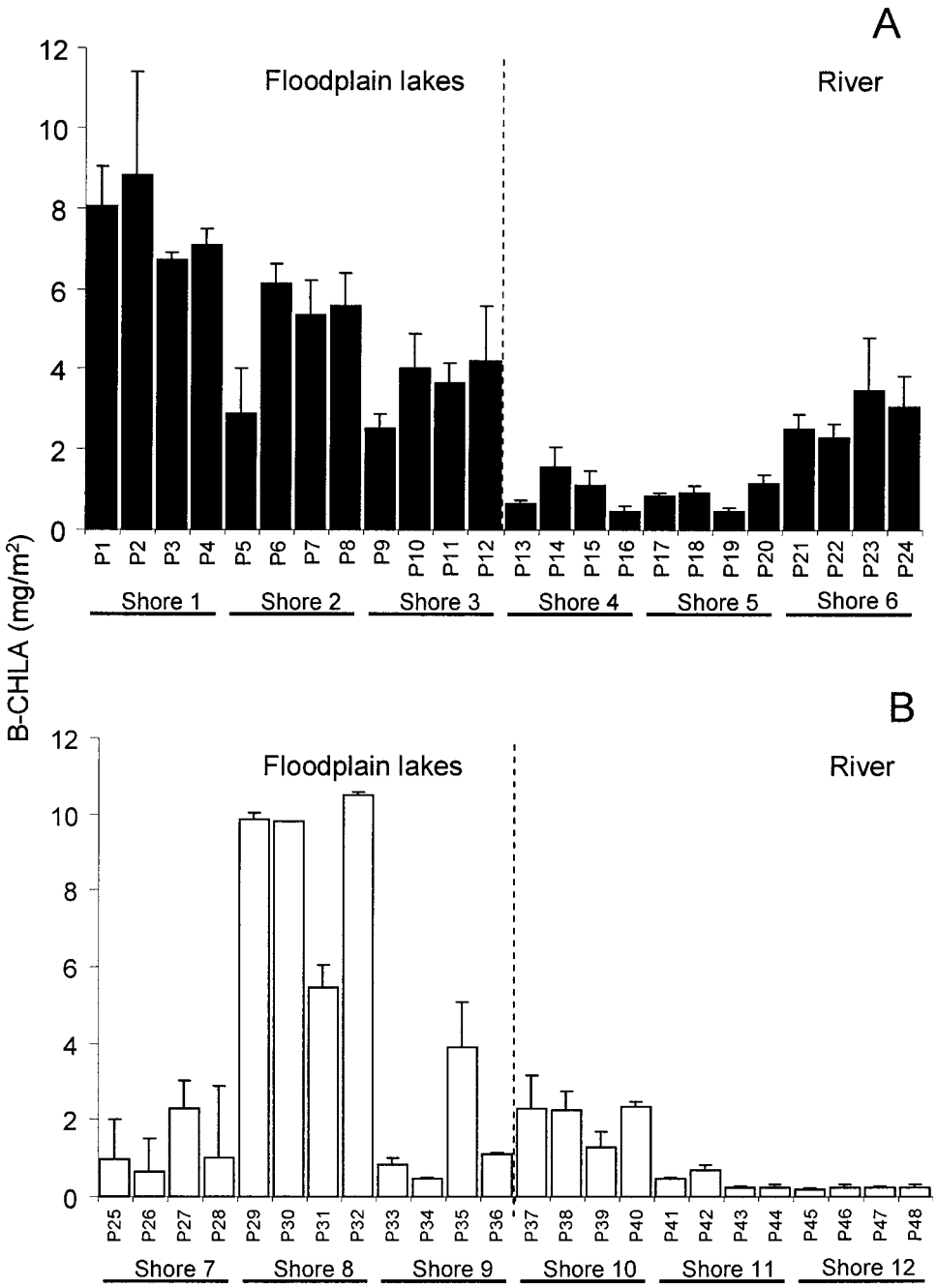

FIG. 7. Mean (+1 SE) benthic chlorophyll *a* (B-CHLA) per plot (P1 to P48) in each shore (shore 1 to 12) during March (A) and May (B) 2002. There were 3 samples (Petri dishes) in each of 4 plots in each of 3 shores in each habitat of the floodplain section. Vertical dashed lines separate floodplain lake and river shores.

measured as well as with algal biomass in littoral zones of the main channel and floodplain lagoons of the Cinaruco River. Major limnological shifts associated with seasonal changes in water level have been documented for other floodplain systems in the Neotropics (e.g., Hamilton and Lewis 1987, Forsberg et al. 1988). In the Cinaruco, seasonal variability in physicochemical variables was consistent with effects of dilution with increasing water level and concentration effects during water recession. Conductivity values in the Cinaruco were among the lowest values recorded for rivers draining large watersheds in the Neotropical region. Among the left-bank tributaries of the Orinoco, the Cinaruco has the lowest reported values for conductivity, alkalinity, turbidity, and concentration of total suspended solids (Depetris and Paolini 1991).

The Cinaruco showed conditions characteristic of an oligotrophic river, and the ecosystem probably is strongly N limited (Cotner et al. 2006, Roelke et al. 2006). Values for DIN and SRP fell within the lower ranges reported for clearwater and blackwater tributaries of the Amazon (Forsberg et al. 1988, Furch and Junk 1997) and Orinoco (Hamilton and Lewis 1990, Vegas-Villarubia and Herrera 1993). However, sestonic chlorophyll concentrations were high during the low-water period. We did not measure total N and P, and it is possible that nutrients associated with a dynamic labile pool of dissolved organic compounds or with the particulate fraction were important for growth of phytoplankton, a phenomenon that has been observed previously (Forsberg et al. 1988, Melack and Forsberg 2001).

We expected DIN and SRP to increase as water level rose, a response that would have reflected decomposition and release of organic matter in flooded areas. Instead, these nutrients peaked ~1 mo after floodwaters had begun to enter riparian forests and savannas. Allochthonous input from the floodplain probably did increase during flooding, but we probably did not detect changes in dissolved nutrients in the water column, in part because of a strong dilution effect and strong biological demands. Allochthonous inputs appeared to be of great importance for the variability of SiO_3 in our study. Sponges were very abundant on trees (JVM, personal observation), so biological demand for dissolved SiO_3 should have increased during the high-water period. In blackwater streams of the Amazon basin, Chauvel et al. (1996) found strong biological control of SiO_3 in the system. SiO_3 dynamics in blackwaters seems to be controlled by biogenic processes (Konhauser et al. 1992, Chauvel et al. 1996).

Stormflow-type peaks in SiO_3 concentration were observed after the first rain storm in the vicinity of the study area. These peaks could have been the result of the transport of high quantities of SiO_3-rich ashes to the water via overland and subsurface flow (McClain and Elsenbeer 2001). Large areas of savanna burn annually during the low-water period, and large inputs of ashes can enrich the water with SiO_3. *Trachypogon* sp., the dominant grass species in Cinaruco savannas, has a high SiO_3 content (7–14%; Mata et al. 1985). Phytoliths are sometimes abundant in sediment samples from lagoons and the main channel of the Cinaruco (JVM, personal observations). A similar situation has been documented for streams draining grasslands and maize cultivars in tropical Africa and, for some of these streams, phytolithic grasses serve as one of the main transport paths of SiO_3 (Bootsma et al. 2003).

Variability in biological variables

Concentrations of both B-CHLA and S-CHLA varied up to one order of magnitude on an annual basis. Phaeophytin *a* concentrations were greater than chlorophyll *a* in the sediments, but not in the water column. Accumulation of senescent benthic algae in the sediment as well as the potentially important deposition of senescent phytoplankton could explain why B-PHAE concentrations were high relative to B-CHLA. We were not able to enumerate benthic algal assemblages at a detailed taxonomic level, but preliminary examination of samples revealed a high proportion of small pennate diatoms and green algae. Microscopic examination of sandy sediments (grain size >63 μm) did not reveal filamentous algae (either Cyanobacteria or Chlorophyta). This sediment fraction retained an unusually high number of large planktonic algal cells, such as *Micrasterias* spp. and *Staurastrum* sp.

Most limnological studies in Neotropical rivers have been conducted in the open-water areas within main channels and floodplain lakes. Interactions among terrestrial and aquatic systems should be greatly magnified at the littoral areas where ecotones between open water and the shore are formed (Ward et al. 1999). Studies on benthic algal biomass in temperate lakes have demonstrated small-scale patchiness (Downing and Rath 1988, Cyr 1998, Kahlert et al. 2002). Our results showed the opposite pattern, with high uniformity at small scales (i.e., within and between plots at the decimeter and meter scale), and larger heterogeneity at large spatial scales. This high level of uniformity observed at smaller spatial scales was unexpected. Two potential factors could be responsible for spatial uniformity of B-CHLA within shores but not among shores. First, water flow and sediment dynamics at a given shore may generate homogeneity in substrate composition and other physical characteristics, which creates relatively large patches of resources required by the benthic algae. We found little evidence of small-scale patches on sandy substrates within the littoral zone of the Cinaruco during the low-water period. However, during the high-water period small-scale heterogeneity was greater than during the low-water period, probably because littoral areas had been inundated only for a short period. During May, scattered shaded areas were interspersed with open areas along the same shore, and littoral zone topography generally was not as uniform as it was during the low-water periods. In addition, higher benthic algal biomass turnover rates during May (Cotner et al. 2006) may have reflected the early succession stage of an algal assemblage domi-

nated by species with higher growth rates and resilience. Autotrophic C inputs from highly productive benthic algal assemblages during early stages of succession would have the potential to affect the entire food web.

A second potential factor that could explain spatial heterogeneity at larger scales, but not at smaller scales, is grazing pressure by detritivorous fishes, especially by *Semaprochilodus kneri*. This species is the most abundant large grazer of organic sediments in the Cinaruco (Winemiller et al. 2006). Strong grazing pressure on benthic algae could override effects of basal resources, such as substrate composition, nutrients, or light, on benthic algal abundance and spatial distribution (Pringle 1996, Flecker and Taylor 2004). Flecker and Taylor (2004) found a parabolic, density-dependent relationship between substrate heterogeneity and a grazer fish in an Andean piedmont stream in Venezuela. According to this relationship, intermediate fish densities accounted for maximum substrate heterogeneity, whereas low and high densities were associated with lower heterogeneity in the distribution of organic matter and benthic algal biomass.

Field observations have shown that not all locations within our study region show the same grazing intensity by detritivorous fishes. In experiments with artificial substrates that were retrieved on a daily basis, we observed grazing activity after only 1 d at some sites, but little grazing activity after as many as 4 d at other locations (JVM, unpublished data). Moreover, relatively high within-treatment, between-location variation was observed in controlled field experiments designed to test fish effects on substrates (Winemiller et al. 2006). Thus, the abundance and feeding behavior of *S. kneri* and other grazing fishes may be influencing seasonal variation in the spatial distribution of benthic algal biomass at intermediate scales within shallow regions of this oligotrophic but species-rich ecosystem.

In conclusion, our study revealed how the spatial and temporal patterns of variation in limnological attributes and algal biomass in the Cinaruco River and its floodplain lagoons are associated with seasonal hydrology. Our analysis of the spatial distribution of epipelic algal biomass suggests a potential interaction between bottom–up and top–down effects on this system, dynamics that are complex in other systems (Hillebrand 2002). Patterns revealed by our descriptive study stress the importance of scale for future research on heterogeneous aquatic ecosystems.

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